VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 2: 73–85
doi: 10.3897/VCS/2021/61463

REVIEW AND SYNTHESIS

Terrestrial biomes: a conceptual review

John Hunter[1], Scott Franklin[2], Sarah Luxton[3], Javier Loidi[4]

1 *School of Environmental and Rural Science, University of New England, Armidale, Australia*
2 *School of Biological Sciences, University of Northern Colorado, Greeley, United States of America*
3 *Northern Territory Government, Darwin, Australia*
4 *Dept. Plant BIology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain*

Corresponding author: John Hunter (jhunter8@bigpond.com)

Academic editor: Melisa A. Giorgis ♦ **Received** 29 November 2020 ♦ **Accepted** 9 June 2021 ♦ **Published** 30 June 2021

Abstract

Aims: We attempt to review the conceptualisation, science and classification of biomes and propose to limit the definition of a biome to potential natural vegetation as determined by general environmental variables.

Results: Classifying the distribution and abundance of vegetation types on earth has been a central tenet of vegetation science since Humboldt's classic studies in the early 1800s. While the importance of such classifications only grows in the wake of extreme changes, this review demonstrates that there are many fundamentally different approaches to define biomes, hitherto with limited efforts for unifying concepts among disciplines. Consequently, there is little congruence between the resulting maps, and widely used biome maps fail to delimit areas with consistent climate profiles.

Conclusions: Gaps of knowledge are directly related to research avenues, and suggestions for defining and classifying biomes, as well as modelling their distributions, are provided. These suggestions highlight the primary importance of the climate, argue against using anthropogenic drivers to define biomes and stabilize the concept of biome to escape from the current polysemy. The last two decades have seen an emergence of new approaches, e.g., using satellite imagery to determine growth patterns of vegetation, leading to defining biomes based on the objective, observable qualities of the vegetation based on current reality.

Keywords

climate, climax vegetation, ecozone, formation, global, potential natural vegetation, terrestrial, typology, vegetation classification, zonal

Introduction

Mapping and classifying the distribution and abundance of the world's organisms, and shifts in their distribution and abundance, is the only means to understand species' response to numerous factors stressing those organisms (climate change, pollution, habitat loss, etc.). Examining species' distributions has been a central tenet of the organismal sciences for 200 years, with the understanding that distributions follow rules and that if we can model those rules, we can predict responses to changes as well as look back historically (e.g., shifts during the Pleistocene, Davis and Shaw 2001; Loidi et al. 2012). Concepts like biomes (developed throughout this review and defined under **Final remarks**), ecozones, and formations have described such distributions at the regional and global scale due to the importance of this global scale for conservation biology (Chytrý et al. 2020) and answering basic ecological questions (Mucina 2019). For example, the biome concept has been used to examine diversity-productivity (Madrigal-González et al. 2020) and species-area (e.g., see Dengler et al. 2020) relationships, quantify temporal dynamics (Wang and Fensholt 2017), model historical distributions and shifts following climate change (Rowland et al. 2016),

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and identify areas most affected by human impact and showing evolutionary convergence in plant form and function (Ringelberg et al. 2020). Indeed, our need for understanding regional distributions is growing quickly as we struggle to understand the effects of a rapidly changing climate, land use changes and other anthropogenic impacts on ecosystems (Shukla et al. 2019). While some of the major drivers of distributions (i.e., 'the rules') have been identified (e.g., climate factors and phylogeny), and those drivers have been related to certain biota (e.g., southern hemisphere taxa) and biotic traits (e.g., life form, growth form and life history), an accepted classification and map are lacking (Moncrief et al. 2015; Higgins et al. 2016). That is, we have yet to define these regional distributions with metrics and subsequently map the world's biomes, despite the obvious and pressing need. One reason is that the knowledge and tools for such work have recently exploded and a concerted effort to incorporate these many new ideas has not been achieved (although see Mucina 2019 and Procheş 2020). Toward that goal, we attempt to review here the history, science and classification of biomes and biome-like concepts and propose a conceptual frame in order to build a global biome classification usable for mapping.

Vegetation biomes: a conceptual review

We first show the development of the biome concept, then the historical antagonism between the two main approaches to delineating biomes (floristics and physiognomy), and then focus on the development of the physiognomical approach and from that approach to the concept of a biome.

Initial steps – from phytogeography to the biome concept

A biome is a complex concept with no exact definition, some have argued that the varying traditions and usages of 'biome' and its synonyms are ambiguous and therefore of little empirical use (Kreft and Jetz 2010). However, the term is continually being adapted and re-invented (Griffith et al. 2019; Keith et al. 2020), and others suggest that much use can come from this flexibility of definition (Pennington et al. 2004). Although the earliest endeavors did not use the term biome, phytogeography, and vegetation science in general, attempts to find general patterns that explain the distribution and interactions of living organisms with the physical and non-physical world. Though not conceptualized at the time as we understand biomes today these early phytogeographical concepts underpin the earliest attempts at biome like concepts. This process involves the discovery of universal laws that govern their lives, imposing an order upon the huge number of species and diverse life forms at different scales. Since the inception of phytogeography, Alexander von Humboldt showed an obsession for finding these patterns and laws (in contrast with systematic Botany and Zoology). The idea of unity in the universe (Cosmos) underlies all his work, so that the multitude of life forms are subject to a unified system of laws that order and govern them in harmony with the physical environment.

"*Die Natur ist für die denkende Betrachtung Einheit in der Vielheit, Verbindung des Mannigfaltigen in Form und Mischung, Inbegriff der Naturdinge und Naturkräfte, als ein lebendiges Ganzes. Das wichtigste Resultat des sinnigen physischen Forschens ist daher dieses: in der Mannigfaltigkeit die Einheit zu erkennen; von dem Individuellen alles zu umfassen, was die Entdeckungen der letzteren Zeitalter uns darbieten; die Einzelheiten prüfend zu sondern und doch nicht ihrer Masse zu unterliegen: der erhabenen Bestimmung des Menschen eingedenk, den Geist der Natur zu ergreifen, welcher unter der Decke der Erscheinungen verhüllt liegt.*"

"*For the thinking consideration, nature is unity in the multiplicity, the connection of the manifold in form and mixture, the embodiment of natural things and forces of nature, as a living whole. The most important result of sensible physical research is therefore this: to recognize unity in diversity; to embrace of the individual all that the discoveries of the latter ages present to us; to scrutinize the details, and yet not to succumb to their masses: remembering the sublime destiny of man to grasp the spirit of nature, which lies hidden under the cover of the apparitions.*" (Humboldt 1855: 5–6).

Consistently, in his comments about plant geography, he addresses:

"*La géographie des plantes fournit des matériaux précieux pour ce genre de recherches: elle peut, jusqu'á un certain point, faire reconnoître les îles qui, autrefois réunis, ce sont sépareés les unes des autres; elle announce la séparation de l'Afrique de l'Amérique méridionale s'est faite avant le dévelopemant des êtres organisés. C'est encores cette science qui montre quelles plantes sont comunes à l'Asie orientale et aux côtes du Mexique et de la Californie; ".*

"*The geography of plants provides valuable materials for this kind of research: it can, up to a certain point, make known the islands which once united are separated from each other; it announces the separation of Africa from South America was made before the development of organized beings. It is still this science which shows what plants are common in East Asia and the coasts of Mexico and California; …*" (Humboldt and Bonpland 1805: 19).

Biome and biome-like systems such as found in many biogeographic or ecoregional classifications attempt to divide and explain the distribution of the world's biota at large scales, allowing global predictions, agreements and assessments, and to act as templates for research and enquiry. While the definition of a biome and its wider usage has a relatively recent history, biome-like schemas extend back to Humboldt's passionate beginnings and inform how we conceptualise the term today.

Historically, biome and biome-like concepts have both variously separated and combined vegetation and fauna

into different, but often parallel schema. Within this review, we concentrate primarily on vegetation, and a schematic presentation of the different contributions along the history related to the biome concept is provided in Table 1. The earliest attempts at a biome vegetation classification were simply to aid in the description of the world's vegetation, to better comprehend where, and potentially why, vegetation occurred in that precise context. Predating Darwin, some tried to explain differences through concepts such as special creations (Egerton 2018). From these descriptive beginnings, however, global schemas have evolved to incorporate our increased understanding of the complexity of abiotic influences on flora. These include climate, soil and disturbance effects (fire, top-down grazing and extreme weather events such as cyclones) as well as human-induced change, and of course natural selection factors driving evolution: phylogenetic constraints, plate tectonics, past climates and disturbance, plus the theoretical importance of scale and feedback mechanisms between the biotic and abiotic realms (Levin 1992).

Evolution works in two key ways to determine the distribution and abundance of organisms: 1) speciation where organisms more geographically adjacent tend to be taxonomically similar (e.g., floristic regions and phytogeography; Burbidge 1960; Takhtajan 1961; Cox 2001; Kreft and Jetz 2010), and convergent evolution that determines traits specific to environmental influences (e.g., physiognomy specific to a certain climate; Humbodlt and Bonpland 1805) which is characteristic of biomes. Takhtajan (1961), for instance, developed the concept of 'Phytochoria' based on taxonomic and phylogenetic information with reference to endemism, harking back to the original works of De Candolle (1855) and Drude (1884) (phytochoria and flora kingdoms were later revised by Cox (2001). We agree with the approach of Procheş (2020) who clearly separated the phytogeographical approach from that the biome approach (convergent evolution), but the historical development of the biome concept starts with a combination of these approaches to map global distributions and thus there is a need to review the history of phytogeography in the conceptualization of biomes.

The earliest vegetation schema – floristics vs physiognomy (1805)

One of the earliest attempts at a large-scale vegetation schema was a map of the distribution of the flora of France by Lamarck and De Candolle (1805). They used floristic composition, climate and terrain to produce floristic regions or provinces for mapping (see Ebach and Goujet 2006). Different approaches used to create a schema are thus present from the earliest days of the concept, with Lamarck and De Candolle's method diverging from Humboldt and Bonpland (1805), who used the physiognomic traits of major dominant plants rather than composition to describe large-scale phytogeographic units. Humboldt and Bonpland tried to establish generic categories that grouped living beings (particularly plants) according to their physiognomic characteristics (morphologic features also used to classify them taxonomically). They addressed physiognomy as having the unifying value of representing adaptive morphological traits occurring in different lineages, which could then be classified into common categories:

"*quelle différence de physionomie distingue les plantes de l'Afrique de celles de nuveau continent?*

Quelle analogie des formes unit les végétaux alpins des Andes à ceux des hautes cimes des Pyrénées?"

"*What difference in physiognomy distinguishes the plants of Africa from those of the new continent?*

What analogy of forms unites the alpine plants of the Andes with those of the high peaks of the Pyrenees?" (Humboldt and Bonpland 1805: 31).

They finally dare to describe a short number of physiognomic groups that could be used to classify most of the vegetation types on earth:

"*Dans la variété des végétaux qui couvrent la charpente de notre planète, on distingue sans peine quelques formes générales auxquelles se réduisent la plupart des autres, et que présentent autant des familles ou groupes plus ou moins analogues entre eux. Je me borne à nommer quinze de ces groupes, dont la physionomie offre un étude importante au peintre paysagiste.* ".

"*In the variety of plants which cover the frame of our planet, we can easily distinguish some general forms, to which most others are reduced, and which are presented as much by families or groups more or less analogous to each other. I limit myself to naming fifteen of these groups, whose physiognomy offers an important study to the landscape painter.* ... (nominates 15 physiognomic types for plants)" (Humboldt and Bonpland 1805: 31) which are later more widely described in a specific paper (Humboldt 1806).

The development of the physiognomic approach

The concept of formation, initially introduced by Grisebach in 1838, defined as "*a major kind of plant community on a given continent, characterized by physiognomy and a range of environments to which that physiognomy is a response*" (Beard 1978), is related to environmental conditions and can even be considered as an expression of them. It can be considered an antecedent of the concept of biome, due to its geographical transversality. For instance, grassland is an herbaceous vegetation dominated by grasses or grass-like plants, and there are several types of them in the world, e.g., tropical C_4 grassland (savanna), temperate dry C_3 grassland (steppe) or alpine meadows. The differences among them rely on the climatic conditions they live, not in the physiognomy, which can be quite similar. At broad scales, climate is the main driver and under similar climatic conditions in different parts of the world, dominant vegetation can be expected to have the same physiognomic types. In fact, the convergence in physiognomy of major vegetation types is now expected to occur if they live under similar broad environmental conditions.

Table 1. Historical development of vegetation-based biome and biome-like concepts.

Author	Biome concept	Conceptualisation	Hierarchical
Lamarck (1778)	Floristic region	Floristic composition (within France)	No
Humboldt and Bonpland (1805)	Phytogeography	Physiognomy of dominants	No
Lamarck and de De Candolle (1805)	Floristic province	Floristic composition, climate and terrain (within France)	No
De Candolle (1820)	Biogeographic region	Composition, endemism and climate.	No
Grisebach (1838)	Formation	Physiognomy	No
Henfrey (1852)	Phytogeography	Composition, taxonomy and geology	No
De Candolle (1855)	Station	Composition, taxonomy, endemism and climate	No
Humboldt (1855)	Phytogeography	Physiognomy	No
Engler (1879)	Kingdom, realm	Composition and climate	Yes
Drude (1884)	Kingdom	Endemic plant families	No
Grisebach (1884)	Formation	Physiognomy	No
Tate (1889)	Bioregionalisation	Taxonomy and climate	No
Merriam (1892)	Life zone, habitation and regions	Distribution of biota, climate and terrain	No
Warming (1895)	Phytogeography	Physiognomy	No
Schimper (1903)	Formation	Physiognomy and climate	No
Diels (1908)	Realm	Physiognomy and climate	Yes
Brockman-Jerosch and Rübel (1912)	Formation, Class	Physiognomic	Yes
Rübel (1930)	Formation, Class	Physiognomic	Yes
Köppen (1931)	Climatic zone	Climate but influenced by distribution of vegetation	No
Tansley (1935)	Biome and Ecosystem	Only biotic – all organisms Ecosystem includes biotic and abiotic	Yes
Carpenter (1939)	Biome	Biotic components	No
Clements and Shelford (1939)	Biome	Composition	Yes
Richards et al. (1940)	Phytogeography	Physiognomy	No
Holdridge (1947)	Formation	Vegetation, temperature, precipitation and evaporation	Yes
Burbidge (1960)	Phytogeographic zone and interzone	Taxonomic (family/genera), climate in particular rainfall seasonality	Yes
Walter (1964)	Vegetation zone	Main vegetation within main climatic zones	No
Crowley (1967)	Ecoregion	Ecologically homogenous region containing a single biome	No
Dashmann (1972)	Phytogeography	Physiognomy of climax vegetation	Yes
Udvardy (1975)	Biome	Physiognomy of climax vegetation, though major biome disjunctions based on flora and fauna	Yes
Box (1981)	Biome	Plant functional types based on climatic limits (expert knowledge)	No
Polunin (1984)	Ecobiome	Biotic, edaphic and climate	No
Walter (1985)	Zonobiome	Biotic, climate	No
Bailey and Hogg (1986)	Macroecosystem	Macroclimate, physiognomy of climax vegetation, landform, attitude	No
Takhtajan et al. (1986)	Phytochoria	Phylogenetic. Taxonomy (orders, families, subfamilies and tribes), endemism	Yes
Prentice et al. (1992)	Biome	Mechanistic tolerances of a small number of lifeforms. Cold, heat and moisture	No
Cox (2001)	Phytochoria	Re-evaluation of Takhtajan (1986)	Yes
Olson et al. (2001)	Biome – Ecoregional	Based on compilation of preexisting units and expert opinion	Yes
Pennington et al. (2004)	Biome	Physiognomy	No
Woodward et al. (2004)	Biome	Physiognomy and phenology as assessed by remote sensing. Climate envelopes and geography	No
Box and Fujiwara (2005)	Biome	Physiognomic	No
Bond et al. (2005)	Biome	Fire as a controlling factor of physiognomy	No
Abell et al. (2008)	Ecoregion	Vegetation type, physiography and climate	No
Crisp et al. (2009)	Biome	Phylogenetic	No
Ellis and Ramankutty (2008)	Anthrome	Inclusion of anthropogenic disturbances	No
Kreft and Jetz (2010)	Bioregionalisation	Species turnover and taxonomic distinctiveness	Yes
Reu et al. (2011)	Dynamic Global Vegetation Model	Plant functional and species richness. Functional type derived from demonstrated trade-offs	No
Scheiter et al. (2013)	Dynamic Global Vegetation Model	Modification of DGVM to include community assembly and coexistence theory	No
Pfadenhauer andKlötzli (2014)	Formation	Physiognomic	No
González-Orozco et al.(2014)	Phytogeography	Climate and vegetation.	No
Moncrieff et al. (2015)	Biome	Physiognomy and phenology	Yes
Moncrieff et al. (2016)	Biome	Physiognomy and phenology modified by local, disturbance and biogeographic history	Yes
Buitenwerf and Higgins (2016)	Phenome and Biogeographic Realm	Physiological habitat classes, evolutionary history and taxonomic composition	Yes
Jiang et al. (2017)	Biome	Physiognomy and phenology, temperature, rainfall and climate predictability	No
Mucina (2019)	Biome	Climatic, physiognomy, common selective pressures, evolutionary assembly	Yes

The early use of physiognomic vs floristic traits marked a distinct divergence in methodology that still exists today. Humboldt's (1806) idea of building a general world classification based on the physiognomy of dominant plants strongly influenced European Geobotany as it unfolded during the 19th century.

Developed by the likes of Joseph Dalton Hooker, Arthur Henfrey, Asa Gray and Alphonse De Candolle, early 1800's publications increased the overall understanding of global plant and vegetation distribution (Egerton 2018). De Candolle (1820) created biogeographic kingdoms based on a more complex understanding of composition that included areas of taxonomic endemism within species and genera (with reference to climate); however, no maps were produced. After De Candolle, German phytogeographer August Grisebach made an important step by coining the term *formation*: "*I give the name of phytogeographical formation to a group of plants, such as a meadow or a forest, that has a fixed physiognomic character* (Grisebach 1838)". This purely physiognomic concept could be applied at different scales, including the global scale, as he did later in his synthesis of the vegetation of the world (Grisebach 1884). The formation concept was accepted by the German-Central European geobotanical tradition throughout the 19th and early 20th century, and synthesis at the global scale continues.

Following the floristic-physiognomic divide, systems were created, with occasional meetings of both.

While Grisebach (1838) and Humboldt (1855) continued the new tradition of using physiognomic criteria, Henfrey (1852) in producing the vegetation of Europe, and De Candolle (1855) in creating his two-volume treatise on plant geography, continued to emphasize floristic composition with reference to climate and geology. In 1879, Engler took a Darwinian perspective to De Candolle's (1855) climate and floristic criteria, adding physiognomic criteria to create four global 'Realms' with 32 regions. Drude (1884) also continued De Candolle's tradition, but concentrated on endemic families to define phytogeographic kingdoms, rather than genera and species. Tate (1889) created the first bioregionalization using taxonomic distributions and climate. While in 1892, Merriam followed, using a systematic method to create a map of life zones based on the composition of the biota, climate and terrain. This allowed for the creation of 'habitations' and 'regions' in a similar fashion to the 'floristic provinces' of Lamarck and De Candolle (1805) and De Candolle's (1855) 'stations'. Drude (1887, 1890) defined the worlds "zones of vegetation", emphasizing that "*Die Vegetationszonen vereinigen die physiognomischen Hauptgenossenschaften der Pflanzen*", "*The vegetation zones unite the main physiognomic associations of plants*".

As a result of this 19th century European work, the formation idea was applied generally to create large-scale units characterized by the physiognomy of the dominant plants. These units could be used to synthesize vegetation at a global scale by describing potential natural vegetation in a broad sense, and correlated with the corresponding broadly defined climatic types. Schimper used Grisebach's (1884) physiognomic 'formations' to produce a map of the globe based on three main levels of vegetation formation: woody, grassy and desertic (Schimper 1898; Schimper and von Faber 1935) (see also Diels 1908). Additionally, these post-'origin of the species' plant geographers were freed from issues associated with vastly different species occurring in different regions of world, which had made comparisons among regions difficult. This change in understanding allowed later physiognomic plant geographers to contemplate more directly on convergence of functional traits.

At the turn of the 20th century, Warming (1895), Schimper (1903) and Diels (1908) moved away from these compositional and taxonomic traditions and emphasised physiognomy over floristics (phytosociology), which was to be the major focus for several decades. Warming, who had re-defined the formation as "*an expression of certain defined conditions of life and is not concerned with floristic differences*" (Warming 1909), was the first to separate floristic composition from physiognomy. This meant that taxonomically distant plants could bear physiognomic traits in common and a vegetation type could be defined by the physiognomy of the dominant species. The formation concept, in this physiognomic sense, was then also adopted by French and Spanish plant geographers and vegetation scientists (Flauhaut 1901: Huguet del Villar 1929; Font Quer 1953; Rivas-Martínez 1996).

Continuing into the 20th century, Brockmann-Jerosch and Rübel (1912), later amended and completed by Rübel (1930), grouped basic units into three main structural levels called associations, but also made *formation classes* (*Formationsklassen*) to highlight their physiognomic nature. Rübel's (1930) description of world vegetation into 'formations' was based on the climatic limits of the main structural elements, which was the first attempt to set limits on the climatic ranges of the types described (Box and Fujiwara 2005). This system, in which units are strongly linked to climate, is included in a series of Botany teaching books by Strasburger (Ehrendorfer 1971) and in the Spanish textbook by Losa et al. (1974). A more recent valuable approach for world-scale formations is that of Schmithüsen (1976), which has been adopted in the last versions of the Strasburger book (Körner 2002). In recent years, these concepts were applied in a new map of the world by Pfadenheuer and Klötzli (2014) with an accurate typology fitting the climatic boundaries. All the vegetation typologies used in these contributions are inescapably based on physiognomy. Today, the formation concept is still important, and one of the largest units in the European, American, Asian and Australian vegetation classification systems (Peet and Roberts 2013; Bolton et al. 2017).

Mid-1900 physiognomic traditions still held a highly deterministic climate-vegetation worldview, without taking into account the evolutionary history of a region (Moncrieff et al. 2016). This was despite the different patterns of existing formations in the northern and southern hemispheres, which had already been noted almost 100 years earlier (Wildenow 1811). Köppen (1931) developed climatic zones of the world based on major vegetation boundaries in relation to seasonality. Meanwhile Hol-

dridge (1947) built on Rübel (1930) and Köppen (1931) to determine the climatic limits of biological processes associated with major plant forms. Using three climatic parameters, biotemperature, mean annual precipitation and potential evapotranspiration ratio, he defined 39 'life zones' (Holdridge 1947). However, as discussed by Moncrieff et al. (2015), climate was often considered in a circular way, both being part of the definition while also used to determine the limits and responses of vegetation. Interestingly, the EcoVeg approach has the top three levels of the hierarchy based on formation concepts, the lowest of those three levels with the name Formation (Faber-Langendoen et al. 2012). This Formation concept integrates growth form and global climates as modified by regional edaphic factors, attempting to satisfy some of the issues discussed above.

"Formation: A vegetation classification unit of high rank (3rd level) defined by combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions". (Faber-Langendoen et al. 2012).

From physiognomy to biomes

Clements was the first to use the term 'biome' as early as 1916 in a meeting of the Ecological Society of America (Clements 1917), initially meaning only a biotic community excluding climate and edaphic components (Pennington et al. 2004), but later it was upgraded to encompass large geographical scale, was largely based on plant formations, and included animals, particularly "influent" animals (Shelford and Olson 1935). Similarly, Tansley (1935) equated biomes to only the biotic components and used biotic and abiotic elements to help differentiate the lower strata of 'ecosystems' within biomes. It was therefore Schimper (1903) who was the first to develop a concept closest to a modern conceptualisation of biomes, when he based his classification on climates selecting for a similar plant form. This first use of the term was somewhat different to many of the later circumscriptions and it was only widely utilised after Clements and Shelford (1939). In contrast to this early definition of a biome, the term has since come to commonly incorporate physiognomic rather than taxonomic or geographical components, and to include climate as the principal determinant of global vegetation distribution (Neilson et al. 1992; Pennington et al. 2004).

Vegetation units at the world-scale are therefore made by grouping together similar formations from different continents, and have been termed formation or biome-types (Beard 1978).

Differences within defined biomes became a major source of contention within the 1970s with Dashmann (1972) defining types based on the physiognomy of the potential climax vegetation, also called potential natural vegetation. This concept was also used by Udvardy (1975) and also by Bailey and Hogg (1986). Extending this, Walter (1985) modified the formation system and coined the concept "*Zonobiome*", of which only nine are recognized globally. Walters large-scale units are basically defined by the climatic zones of the world and act as containers for the existing ecosystems.

One of the major issues, apart from the generalised attempts of Holdridge (1947), is that these high-level classifications have been expert-based and deterministic in approach. The reliance on intuition and personal experiences of the creators of each system greatly limits our ability to compare schema and to perform statistical stratifications testing theory (Moncrieff et al. 2014). In a comparison of different biome classifications, Moncrieff et al. (2014) discovered that different biomes in different continents had different environmental envelopes and that these could vary more within than between biomes, potentially due to past histories. To provide a sounder underpinning to biome creation, a more functional approach in which underlying processes are emphasised became the focus in recent decades (Griffith et al. 2019).

Challenges to a Global Biome Classification

This conceptual review demonstrates that there are many fundamentally different ways to define biomes, hitherto with limited efforts for unifying concepts among disciplines. Consequently, there is little congruence between the resulting maps (Higgins et al. 2016), and widely used biome maps fail to delimit areas with consistent climate profiles (Moncrieff et al. 2015). The approach of the formation concept by Faber-Langendoen et al. (2012), EcoVeg, integrates growth form and global climates as modified by regional edaphic factors but is not yet in a form that can be modelled. The highly clarifying contribution of Procheş (2020) establishes the concept of biome clearly separate from biogeographic concepts such as phytochoria.

Other recent challenges to the biome concept include the finding that vegetation structure and function of the same biome on different continents can differ substantially; for example, savannas (Lehmann et al. 2014; Moncrieff et al. 2016; Muldavin et al. 2021). Moreover, under the same climatic conditions, different plant formations such as savannas and tropical deciduous forests are possible. These alternative states are modulated by complex interactions between climate, soil conditions, herbivores or disturbances such as fire (Breckle 2002; Bond et al. 2005; Moncrieff et al. 2016; Langan et al. 2017). In the case of alternate states under the same climate, one also needs to decide whether these two formations represent one or several biomes. An additional dilemma is that there is no agreement regarding which kinds of edaphic, hydrological, orographic or disturbance-driven deviations should be considered important enough to count them as separate biomes. For example, Olson et al. (2001) recognize mangroves as a biome but not riparian forests. Likewise, mountain areas with their compressed sequence of vegetation belts are not treated consistently and are often simply

overlooked (Woodward 2004) or included into a general category (Mucina 2019) most likely due to spatial representation. Lastly, as humans have shifted the biosphere into a new geological epoch, one can question whether it still is appropriate to consider only the potential natural vegetation in a biome map (Ellis et al. 2010; Ellis 2011). The idea of Ellis (2011) to add degree and type of human alterations as an additional dimension to a revised biome concept is appealing.

It has become apparent that a close one-to-one relationship between climate type and physiognomic types has some weaknesses, as different floras show disparity from predicted convergence. For example, the asymmetry between Northern and Southern Hemispheres was initially pointed out by Willdenow (1811), who focused primarily on the floristic differences between hemispheres, rather than on vegetation *sensu stricto*. This dissimilarity was extensively addressed by Troll (1948) who published his famous average continent, and later by Box (2002), who argued that under similar climatic envelopes, particularly under non-tropical conditions, the physiognomy of vegetation is often different between the latitudes. This dissimilarity is more pronounced in extratropical areas and is in contradiction with the principle of 'similar-climate, similar-physiognomy'. Thus, climatic differences between the halves of the planet do not sufficiently explain vegetational divergences, and it is likely that a long period of separation and evolutionary history plays a major role in floristic-phylogenetic dissimilarities (Hopper 2009).

The necessity to consider physiology and plant functional types became apparent. Box (1981) attempted to define more precisely the physiological limits of major plant forms and developed an understanding of plant functional types based on physiological limits imposed (largely) by climate. He defined one hundred plant functional types based on climatic filters and used to create biome types based on a culmination of the types available within zones. The advancements in physiological classifications using plant functional types and climate were still, however, formalised within a deterministic framework largely informed by expert opinion (Ni 2001; Bunce et al. 2002; Reu et al. 2011; Lehmann et al. 2011; Moncrieff et al. 2015). Additionally, in spite of these developments in our understanding of physiological tolerances and functional types, a resurgence of purely floristic and compositional approaches also occurred around this period (1980's).

In recent studies, the importance of phylogeny and floristic divergence in producing different physiognomic profiles within similar climatic envelopes has been highlighted (Pennington et al. 2004; Moncrieff et al 2014, 2015). Plant traits are not only determined by current environmental conditions, but are also the result of inherited ancestral adaptations to past conditions, i.e. "niche conservatism" (Donoghue 2008; Crisp et al. 2009; Loidi 2018). The divergent physiognomy observed in the altitudinal belts of mountains between different geographical areas provides an example. Zonation in tropical mountains does not match the well-known model for temperate and Mediterranean mountains, as initially pointed out by Humboldt. While climatic differences due to latitude could explain part of these differences, we cannot ignore the floristic-phylogenetic divergences (Troll 1961: Stocker 1963) and that additional abiotic and biotic interactions are likely important in driving the evolutionary pattern.

Beyond evolution

The underlying principles of strict relationships between climate and vegetation used to develop the majority of earlier schema have been re-evaluated by a number of researchers. Bond et al. (2005) showed that fire was a controlling factor in the distribution of physiognomic types across large areas of the world and this helped to explain some of the anomalies encountered under purely deterministic approaches. Crisp et al. (2009) showed that phylogenetic history and continental movements constrained the expression of plant functional types limiting the direct relationships between climate and functional types. Phylogenetic lineages were rarely found to colonise new biomes (Crisp et al. 2009). Montcrieff et al. (2016) highlighted that not only did evolutionary and biogeographic history limit functional convergence, but that ecosystem engineering could occur due to feedbacks between vegetation and climate along with disturbance, thus altering the conditions for plant function influencing the expression of traits. Top-down pressure from large herbivores was shown to alter the combination of traits expressed beyond the effects of climate or local edaphic conditions (Lehmann et al. 2011).

Anthropogenic influences were also considered important to the extreme they severely influence a majority of terrestrial ecosystems of the world. The term "anthromes" has been coined to designate human influenced systems (Ellis and Ramankutty 2008). Clark et al. (2010) suggested that natural selection factors or competition could exceed the influence imposed by climate on composition and expression of functional traits. Further, Jiang et al. (2017) proposed the importance of climatic fluctuations and predictability, and their complexity, as being highly relevant to the structure and functioning of vegetation types, which could also explain divergences based on average climate records. Plants require different strategies and tactics to cope with differing levels of predictability within their environment (Jiang et al. 2017). The non-deterministic nature of plant functional responses provided evidence that alternative stable states of biomes may occur within the same location and under the same climatic conditions, dependent on historical and current influences (Bond et al. 2005; Lehmann et al. 2011; Buitenwerf and Higgins 2016; Moncrieff et al. 2016).

With improved access to geographical information systems and higher computing power over the last two decades, an emergence of more top-down approaches to defining the boundaries of major vegetation types and biomes became a possibility. Such approaches were able to use satellite imagery to determine growth patterns of vegetation, for example NDVI, leading to defining biomes

based on the objective, observable qualities of the vegetation (Pennington et al. 2004). Woodward et al. (2004) assessed physiognomic and phenological types based on climate envelopes using remote sensing. Such approaches were viewed as a progress as they allowed interpretation without circularity, but also placed the focus on existing vegetation compared to potential. With global databases, satellite imagery and GIS abilities, more intensive and complex interrogation of global patterns and species functional responses have become achievable. Dynamic Global Vegetation Models (DGVM) were first used by Prentice et al. (1992), who argued that models based on deterministic considerations would be more robust than those based on correlations. Reu et al. (2011) extended the DGVM concept by investigating the survival of plant functional trade-offs across a range of global conditions and regional climatic constraints. Scheiter et al. (2013) proposed that, in order to move away from the fixed plant functional type paradigm, DGVMs should be based in community assembly, competition and coexistence theory.

Final remarks

In this section we offer a summarized conceptual proposal of the term Biome. The proposal combines historic evolution with more recent contributions to the concept, trying to safeguard a necessary stability in the use of the term in order to prevent a "babelization" which we consider entirely inconvenient. In science, concepts can evolve, while avoiding change to the original conceptual underpinnings (semantic area). Similar to the term "species", which has been used for centuries while the information carried in it has increased enormously (from morphology to current genetics), but we apply it to the same objects as the ancient botanists. If there is a horizontal displacement, i.e., a change in the group of objects included within the concept, excluding some objects and including new objects, that is a change in the meaning (semantic area) and confusion is likely. Science has to stick to the highest terminological accuracy so that the well-known concepts can be enriched but not changed. If there are new concepts, new terms have to be coined to name them. In the case of biome, the most recent version of this term appearing in the literature is that of the Global Ecosystem Typology, issued by the IUCN (Keith et al. 2020). In it, the term biome (functional biome) is used for level 2 of the proposed classification and is based on an imprecise definition with conditions such as "main ecological drivers" and "main ecological functions". Of the seven biomes recognized for the terrestrial domain (1-tropical-subtropical forests, 2-temperate-boreal forests and woodlands, 3-shrublands and shrubby woodlands, 4-savannas and grasslands, 5-deserts and semi-deserts, 6-polar-alpine, 7-intensive land-use systems), only four, 1, 2, 5 and 6, are determined by climate in a very loose way. Two others are largely miscellaneous units composed by vegetation types representing seral stages associated with disturbance regimes, often fires, and the last one is the unstable and heterogeneous "biome" of intensive land use systems. This conception of biomes is far from the ones based on a climatic or on stable environmental factors determinism. Additionally, different criteria are adopted for the biome definitions (Keith et al. 2020): climate, disturbances, human influence, and that could be considered a source of inconsistency. If a new conceptual entity is proposed, perhaps a new name should be proposed to avoid confusion.

The inclusion of human influences in the conceptual framework of biome has the following objections:

Human influence is relatively new, with notable influences on terrestrial ecosystems beginning approximately 11,000 years ago when the Neolithicum age started and agriculture and cattle raising arose (Lubbock 1913). Before that point, the impact of humans was that of a medium-sized mammal. After that time, these activities expanded throughout the world at very different paces and intensities, transforming the territories in numerous ways, but global change has only occurred in the last few hundred years. In any case, human influence in terrestrial ecosystems has been and is enormous, and manifests in a complexity of ways, depending on geographical conditions, technology and cultural variability.

In addition, the way in which humans have influenced ecosystems has also been heavily influenced by the natural conditions inherent to them. This has to do with profitability of the environment in question; with humans particularly concentrating modifications within highly fertile environments and leaving highly infertile landscapes much less disturbed (YODFELS as opposed OCBILS of Hopper 2009; Hopper et al. 2021). For example, compare and contrast human occupation and use within deserts with the seasonal tropical forest, or on the tundra with the Mediterranean evergreen sclerophyllous forest areas. Modern technology is pushing towards a homogenization of the land uses and species composition and thus of the ways that humans transform natural ecosystems. We can nearly grow tomatoes in the Arabian desert by means of intensive irrigation and we can grow oranges in the tundra if we provide a formidable greenhouse and fertilizers. Thus, human influence is very diverse and is changing with technology, population growth and time and space. We therefore propose that human influence should not be considered as a defining element for biomes and that the creation of Anthromes is counterproductive (Ellis and Ramankutty 2008; Ellis 2013). Concepts that include the influence of humans within a definition of a biome such as anthromes are likely to have a blurring effect that will only be temporary in nature as technology and human uses advance and change over the decades. The biome should be a concept restricted to nature in the first instance. If we do so, we can use the biome concept to assess the degree and type of human alteration on a given site just by comparing with the corresponding biome. This has been also argued in favour of the Potential Natural Vegetation concept (Loidi and Fernández-González 2012).

Another point is disturbances as a main factor in defining biomes. This is also ill-defined because many of these disturbances are human induced (e.g. grazing, browsing, etc.) or the disturbance regime was altered. We need to take particular care if considering the use of disturbances as separating nature versus human disturbances can be highly complex.

The numerous challenges for developing a global biome classification are synonymous with understanding the diversity of life on earth, which essentially point to knowledge gaps, but those challenges also point to opportunities. In simply trying to understand the diversity of life on earth, Hortal et al. (2015) lists seven shortfalls: (i) Linnean shortfall (not all species have been discovered), (ii) Wallacean shortfall (lack of knowledge of species geographical distributions, especially less common species), (iii) Prestonian shortfall (lack of knowledge about species dynamics in space and time), (iv) Darwinian shortfall (lack of knowledge about evolutionary lineage of species and traits), (v) Raunkiaeran Shortfall (lack of knowledge of ecologically relevant species traits), (vi) Hutchinsonian Shortfall (lack of knowledge about species' tolerances), and (vii) Eltonian Shortfall (lack of knowledge about species' interactions). These gaps of knowledge are directly related to research avenues for defining and classifying biomes, as well as modelling their distributions. Models provide one way to move the concept of biomes forward in testing the concept – testing the importance of variables like climate, disturbance, and phylogeny. Therefore, refining models of biomes toward prediction will allow the concept of a biome to be tested and ultimately define a biome.

In basic agreement with Mucina (2019), a biome is a large-scale container concept that includes a series of elements that belong to these three categories:

- A biome encapsules all the biological diversity that can be found within its limits: plants, animals, fungi, etc.
- A biome encompasses all the forms of assemblages of these species: populations, communities (coenoses), landscapes.
- A biome encompasses the processes taking place in the frame of the two aforementioned components: ecosystem functioning, dynamic processes, evolutionary processes, disturbances, etc.

The limits of a given biome in comparison with neighbouring biomes are given by:

- Physiognomy, dominant life-forms. Deciduous forests vs. evergreen forests, steppe vs. desert, etc.
- Regional climate or climatic zone. Ever rainy tropical vs. seasonally rainy tropical, boreal vs. temperate, summer rainy vs. winter rainy, etc.
- Ecological factors. Soil fertility, natural disturbance regime, etc.

As an integrative concept, the biome should in first principles be defined by natural features: natural biota (flora, fauna, etc.), natural ecosystems, natural landscapes. Natural is considered when human influence is less apparent at the level of noticeable ecosystem modification.

Author contributions

JL and JTH wrote much of the initial draft but all authors JL, JTH, SF and SL contributed greatly to the writing and construction of the final document.

Acknowledgments

JL has been supported by the funds of the project IT936-16 for research groups of the Basque Government.

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E-mail and ORCID

John Hunter (Corresponding author, jhunter8@bigpond.com), ORCID: https://orcid.org/000-0001-5112-0465
Scott Franklin (Scott.Franklin@unco.edu), ORCID: https://orcid.org/000-0003-3922-8857
Sarah Luxton (Sarah.Luxton@nt.gov.au), ORCID: https://orcid.org/0000-0002-4714-9799
Javier Loidi (javier.loidi@ehu.eus), ORCID: https://orcid.org/0000-0003-3163-2409